ACTA PARASITOLOGICA POLONICA
VOL. II WARSZAWA, 21. II. 1955 FASC. 20

Z Muzeum Przyrodniczego Instytutu Zoologicznego Uniwersytetu im. Bolesława Bieruta we Wrocławiu
Kierownik Muzeum: dr Janina Janiszewska

Janina JANISZEWSKA

ACTINOMYXIDIA

Morphology, ecology, history of investigations, systematics, development

ACTINOMYXIDIA

Morfologia, ekologia, historia badań, systematyka, rozwój

ACTINOMYXIDIA

Морфология, экология, история исследований, систематика. развитие

The *Actinomyxidia* are a small and well defined group (order) of the *Cnidosporidia*. They are parasitic in the body-cavity and the gut-epithelium of *Oligochaeta* of the families of *Tubificidae* and *Lumbricidae* and of the *Sipunculoidea*.

Morphology

In the fully grown state the entire body forms a pansporoblast, i. e. a cyst enclosing 8 sporoblastic cells. Out of these cells develop 8 spores of triradial symetry, of which each is furnished with 3 polar capsules containing evertible threads (fig. 7). The spore is formed of sporozoites or a sporoplasm surrounded by two envelopes, the inner or the endospore and the outer or the epispore. The number of sporozoites or nuclei of the sporoplasm, which is a syncytium, is varying and is often characteristic for the species. The sporoplasm or the sporozoites are enclosed in the space surrounded by the envelopes and can assume a globular, barrel-like or cylindrical shape (fig. 2—15). The endospore is made up of 1—2 cells which form the inner envelope around the sporoplasm or the sporozoites. The epispore is triradially symmetric and is formed by 6 cells of which

three occupy the apex of the spore and contain 3 polar capsules. The remaining three build up the rest of the envelope; their shape is diverse and characteristic for several species (fig. 1—15). It is one of the principal taxonomic characters of the genera and species. In some species the spores unite into characteristic figures (*Synactinomyxon*) or nets (*Siedleckiella*) (fig. 4, 7, 9).

The envelope is highly pellucid and therefore often hardly visible and contains protoplasmatic inclusions. Caullery et Mesnil (1905) and Granata (1924) hold the opinion that it subserves nutritive function, i. e. assimilates nutrient substances at the expense of the host and is therefore an assimilatory tissue rather, than a kind of cyst only. The envelope guards the spores from the changing outer conditions. Inside the pansporocyst the spores are closely packed and in some species (e. g. *Triactinomyxon)* the ends of the long processes of the envelope are tucked in to make the surface smaller (fig. 12).

Ecology

In contact with water the envelopes stretch and assume their characteristic shape, serving most probably as a floating apparatus. Kofoid (Doflein 1916) found spores in the plancton. This adaptation to planctonic life is a mean of distribution of parasitic forms, the hosts of which are mostly benthonic animals (*Tubificidae*). The structure of the spores as well as their way to unite in some species into larger wholes are doubtlessly adaptations to ecological conditions and adaptations to the ethology of the host, requisite for a successful infection. The way by which the planctonic spores enter the body of their host is yet unknown. It can be assumed that after a time they must sink to the bottom.

The pansporocysts of some species develop in the body-cavity of the host, of others in the epithelium of his gut. The localization is well defined and constant except in some cases, as for instance *Triactinomyxon magnum* Granata, a parasite of the body-cavity which however is found sometimes also in the gut-epithelium.

Forms attached to the epithelium of the gut cause pathological changes, mostly epithelial hypertrophy leading to a closure of the lumen of the gut (fig. 16a). To the parasites in the body-cavity the host reacts by surrounding them with groups of lymphocytes (fig. 16b). Štolc (1899) observed a decrease of the haemoglobine content in the blood.

The pansporocysts of forms parasitizing in the gut-epithelium fall in the lumen of the gut and then are evacuated together with the faeces, while the pansporocysts of body-cavity parasites reach the exterior only after the death and maceration of tissues of the host or after amputation of the infected part of its body. G r a n a t a has found intact spores of *Sphaeractinomyxon* in putrefying *Limmodrili.* As different developmental stages are found together in infected hosts, e. g. initial stages of gametogenesis as well as end stages with ripe spores, infection most probably is not simultaneous.

It may be however that this lack of simultaneity in development will find a better interpretation unattainable at the present state of our knowledge. Experimental infection attempted by C a u l l e r y and M e s n i l did not yield any results. G r a n a t a thinks that spores must reach a certain state of maturity before infection is possible, most probably they must pass through a resting stage outside the body of the host during which they may be resistent to dessication. Autoinfection of the host is admitted by some authors, ripe pansporocysts falling into the lumen of the gut, bursting there and setting free the spores. These again shed their sporozoites, which might infect other parts of the epithelium of the gut. The fact of empty spore-envelopes being found in the body-cavity or at the base of the epithelium favours that view. The faculty of autoinfection would explain also why there are so few but at the same time heavily infected specimens (L é g e r).

Certain species are found sometimes in great abundance, e. g. N a v i l l e (1930) has found *Guyénotia sphaerulosa* in a great number of *Tubifex,* the worms being at the same time infected heavily, other authors maintain that the *Actinomyxidia* are of rare occurence; D. L. M a c k i n n o n and D. I. A d a m for instance have found only five specimens infected by *Triactinomyxon* in 1,250 uninfected *Tubifex,* Š t o l c only 1 in 300.

The *Actinomyxidia* are little known. They were studied sporadically and occasionally and only by a restricted number of investigators and this may account for the assumption of their rare occurence. It is possible however that the real cause lies in the fact that the *Actinomyxidia* need certain stable ecological conditions, particularly when living outside the body of the host and at the time of infection and so their abundance or scarcity in the hitherto investigated localities depends on the degree of realisation of these conditions.

History of investigation

The *Actinomyxidia* are known since 50 years only. They were first found in Czechoslovakia by Štolc in 1899, who classified them among multicellular, two-layered organism as a new group of *Mesoza*, related to the *Myxosporidia*. Štolc noticed their close resemblance to the spores of *Myxosporidia*, but thought that in the forms newly discovered by him the cells were real tissue cells, while in the *Myxosporidia* they are only part of a unicellular body and he therefore assumed a relationship with the thread-like *Dicyemidae*. Mrázek in 1900 criticized Štolc for lack of knowledge of the recent literature treating of the organisation of *Myxosporidia* and stated the undubitable relationship of *Actinomyxidia* with the *Cnidosporidia*, similar to *Ceratomyxa*. In 1904 M. Caullery and F. Mesnil recognized the *Actinomyxidia* as a separate group of *Cnidosporidia*, of an even rank with *Myxosporidia* and *Microsporidia*.

Štolc discovered in 1899 three genera: *Synactinomyxon*, *Triactinomyxon* and *Hexactinomyxon*. Caullery and Mesnil in 1905 discovered the genus *Sphaeractinomyxon* and described its development, initiating investigations relative to the development of these parasites. In 1912 I. Ikeda found in Plymouth in the body-cavity of *Petalostoma minutum (Sipunculidae)* the genus *Tetractinomyxon* and discerned in its structure a double envelope, the outer of three cells and the inner of one cell, and inside the envelopes a single two-cellular sporozoite (fig. 1). This form with a spore containing but a single sporozoite Ikeda separated from the other hitherto known species, which contain a great number of sporozoites, and created for it a new systematic group the *Simplicia*, while those with a larger number of sporozoites form the group of *Multiplicia*. In 1922 Granata discovered the new genus *Neoactinomyxon* and in 1925 he worked out new systematics of the *Actinomyxidia* recognising two families: the *Haploactinomyxidae* corresponding to the *Simplicia* of Ikeda, and the *Euactinomyxidae* corresponding to his *Multiplicia*.

The group was supposed to differ in the inner envelope, the endospore being present in the *Haploactinomyxidae* and apparently absent in the *Euactinomyxidae*. At that time sporogenesis was still but imperfectly known. Working in 1953 (54) on the sporogenesis of *Siedleckiella* I was able to demonstrate the presence of the inner enve-

List of Hosts

Host	Country	Parasite
Oligochaeta		
Tubificidae:		
Clitelio arenarius Müller	France	*Sphaeractinomyxon štolci*
Peloscolex (Hemitubifex) benedici Udekem	France	*Sphaeractinomyxon štolci*
Limnodrilus hoffmeisteri Clapar.	Italy	*Sphaeractinomyxon gigas*
Limnodrilus udekemianus Clapar.	„	*Neoactinomyxon globosum*
„ „	„	*Triactinomyxon magnum*
„ sp.	Czechoslovakia	*Neoactinomyxon globosum*
Limnodrilus claparèdeanus Ratz.	Poland	*Siedleckiella antonii*
Tubifex tubifex Müller	Czechoslovakia	*Synactinomyxon tubificis*
„ „	France	*Triactinomyxon dubium*
„ „	„	*Triactinomyxon ignotum*
„ „	Luc-sur-Mer (Calvados)	*Guyénotia sphaerulosa*
„ „		
„ „	England	*Triactinomyxon ignotum*
„ „	„	*Triactinomyxon légeri*
„ „	„	*Triactinomyxon mrázeki*
„ „	Poland	*Raabeia gorlicensis*
„ „	„	*Hexactinomyxon hedvigi*
Tubifex ohridensis	Yougoslavia	*Triactinomyxon ohridensis*
Tubifex (Psammoryctes) barbatus Grube	Czechoslovakia	*Hexactinomyxon psammoryctis*
Tubifex sp.	„	*Triactinomyxon ignotum*
„ „	Poland	*Siedleckiella silesica*
Ilyodrilus prespanensis Hrabě	Yougoslavia	*Sphaeractinomyxon ilyodrili*
Lumbricidae:		
Eiseniella sp.	„	*Sphaeractinomyxon danicae*
Sipunculoidea		
Sipunculidae:		
Petalostoma minutum Kef.	England	*Tetractinomyxon intermedium*
„ „	„	*Tetractinomyxon irregulare*

lope in that genus (see, below, chapter on sporogenesis) and by comparing two drawings by other workers of appropriate stages, I become convinced of its presence in the other genera too. This proves the classification into *Haploactinomyxidae* and *Euactinomyxidae* to be inadequate. The division into *Simplicia* and *Multiplicia*, resting upon quantitative differences in the number of sporozoites is superfluous in view of the general uniformity of development.

Other new species and genera and their development have been described by D. L. Mackinnon and D. I. Adam in 1924, by Naville in 1930, J. Georgević in 1938, 1940, O. Jírovec in 1940 and J. Janiszewska in 1952-54. We known at present 9 genera with 21 species of the order *Actinomyxidia*. All these forms were as yet found in Europe only and we have no information grom other parts of the world. [Kofoid (Doflein, 1916) found spores in the plancton in America]. However parasites from this order may presumably live also in other parts of the world as their principal hosts, the *Tubificidae* and *Lumbricidae* are widely distributed the world over.

Systematics

Granata's systematics have been simplified by the present writer in the following way:

Class: *Sporozoa*
Subclass: *Cnidosporidia*
Order: *Actinomyxidia*

Genera: *Tetractinomyxon* Ikeda, *Sphaeractinomyxon* Caullery-Mesnil, *Neoactinomyxon* Granata, *Synactinomyxon* Štolc, *Guyénotia* Naville, *Raabeia* g. n. Janiszewska, *Siedleckiella* Janiszewska, *Triactinomyxon* Štolc, *Hexactinomyxon* Štolc.

Key to the genera:

A. Spore with one twonucleate sporozoite . . . . . (*Simplicia* Ikeda)
. . . . . *Tetractinomyxon* Ikeda

B. Sporoplasm a multinucleate syncytium, or split into many mononucleate sporozoites . . . . . (*Multiplicia* Ikeda)

I. Cells of epispore form a simple membrane without processus
. . . . *Sphaeractinomyxon* Caullery-Mesnil

II. Cells of envelope globular, swelling into rounded discs
. . . . . *Neoactinomyxon* Granata

III. Cells of epispore with processus
a. Two longer, wing-like processes and a short conical processus . . . . . *Synactinomyxon* Štolc
b. Three finger-like processes
1. Processes truncated . . . . . *Guyénotia* Naville
2. Processes pointed, invaginated while in the pansporocyst . . . . . *Raabeia* g. n.
3. Join to form hexahedric net . . . . . *Siedleckiella (antonii)* Janiszewska
c. Cells of epispore anchor-like, with three arms
1. Arms of anchor obtuse join to form hexahedric net . . . . . *Siedleckiella (silesica)* Janiszewska
2. Arms long and pointed . . . . . *Triactinomyxon* Štolc
3. Arms doubled (six arms) . . . . . *Hexactinomyxon* Štolc

I. Genus *Tetractinomyxon* Ikeda 1912.

Epispore tetrahedric without processes. 2 species known.

1. *Tetractinomyxon intermedium* Ikeda 1912 (fig. 1).

The epispore and the endospore are tetrahedric. The nuclei of the epispore in three corners of the base of the pyramid, at its apex are

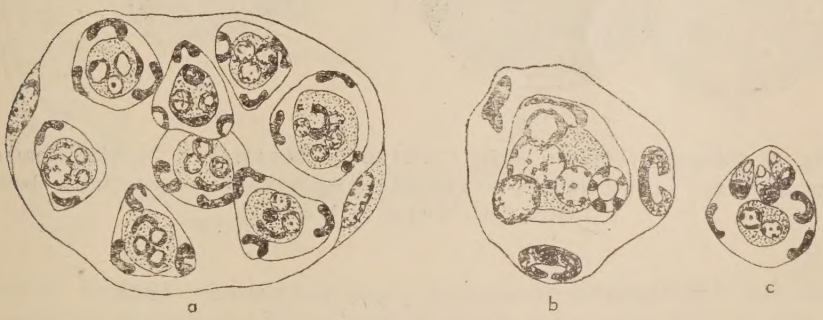

Fig. 1. *Tetractinomyxon intermedium* Ikeda: a — Pansporocyst with eight ripe spores; b — Spore from above, showing exo- and endospore, three nuclei of polar capsules, a binucleated sporozoite and three nuclei of the envelope; c — The same, side-view. After Ikeda.

situated the three polar capsules measuring 5 μ, with three nuclei. Endospore with one nuncleus lies in the epispore with its corners directed towards the middle of the faces of the epispore. The germ is at first mononucleate, then has two nuclei of uneven size. Lives in the body-cavity of *Petalostoma minutum* Kef., found in Plymouth.

2. *Tetractinomyxon irregulare* Ikeda 1912.

Epispore tetrahedric, endospore globular. Their nuclei disappear during development. Lives in the same host. Found in Plymouth.

II. *Genus*: *Sphaeractinomyxon* Caullery-Mesnil 1905.

Epispore without processes. Sporoplasm with numerous nuclei, in the mature state divided into many mononuclear sporozoites. 4 species.

1. *Sphaeractinomyxon štolci* Caullery-Mesnil 1905.

Globular spores of 17—25 μ diameter (fig. 2). Parasite of the body-cavity of *Clitellio arenarius*, O. F. Müller, *Hemitubifex benedeni* D'Udekem. Found in St. Martin, Royan, France.

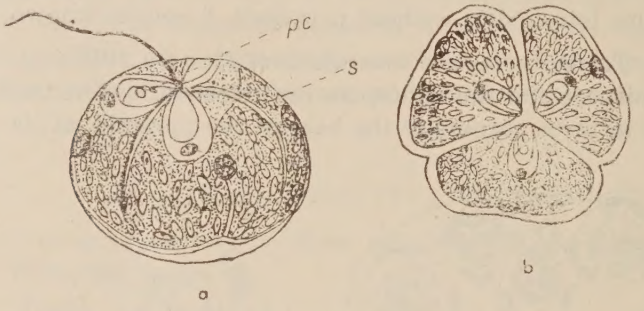

Fig. 2. *Sphaeractinomyxon štolci* Caullery-Mesnil: a — Side-view of the spore, pc — polar capsule, s — amoeboid sprozoite; b — Spore from above. After Caullery et Mesnil.

2. *Sphaeractinomyxon gigas* Granata 1923.

The spore forms a trigonal double pyramid, measuring in cross-section 32—45 μ. Lives in the body-cavity of *Limnodrilus hoffmeisteri* Claparède. Found by Granata in Fiume, Mugnone, Florence (Italy).

3. *Sphaeractinomyxon danicae* Georgević 1938.

Globular, or pear-shaped spores containing 32 amoeboid sporozoites. Parasite in the gut-epithelium of *Eiseniella* sp. Found in Lake Ochrida (Yougoslavia).

4. *Sphaeractinomyxon ilyodrili* Jírovec 1940.

Spore most probably polyhedric measuring in cross-section 15×25 μ. Sporoplasm formed of many sporozoites. Was studied only

on microscopical sections. Parasite in the body-cavity and testes of *Ilyodrilus prespanensis* Hrabě. Found in the yougoslavian part of the Skutari Lake.

III. Genus: *Neoactinomyxon* Granata 1922.

Cells of the epispore are inflated and form 3 globular, inwardly concave discs. Endospore composed of mononuclear globular sporozoites. To date one species known.

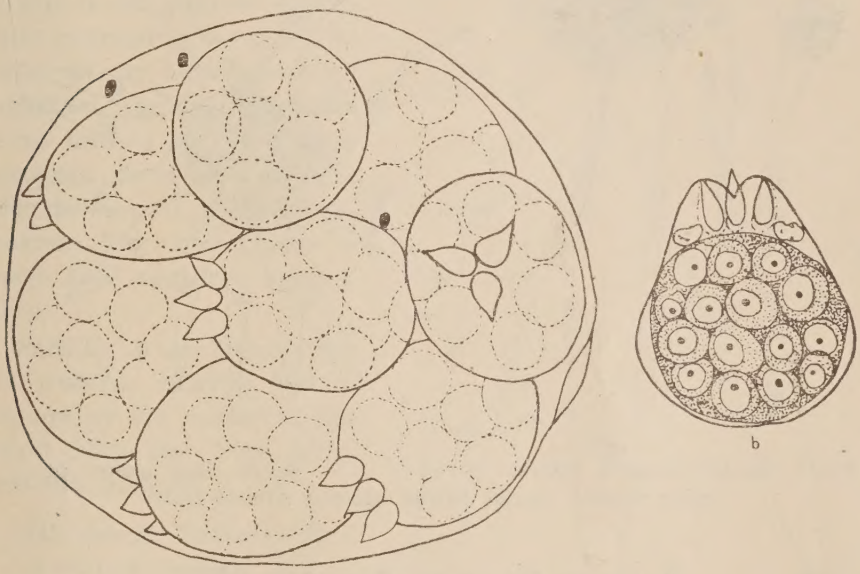

Fig. 3. *Neoactinomyxon globosum* Granata: a — Pansporocyst with ripe spores; b — Side-view of the spore. After Granata.

1. Neoactinomyxon globosum Granata 1922 (fig. 3).

With characters of the genus. Inside the spore 16 sporozoites measuring 15—20×12—16 μ (measured by O. Jírovec). Lives in the gut-epithelium of *Limnodrilus udekemianus* Claparède. Found in Fiume, Greve, Florence (Granata) and in Czechoslovakia (Jírovec).

IV. Genus: *Synactinomyxon* Štolc 1899.

Epispore with two wing-like and one short, conical process, bound together in the pansporocyst by the short conical processes into

a star-like figure (fig. 4). Sporoplasm with many small nuclei. 1 species.

1. *Synactinomyxon tubificis* Štolc 1899.

With characters of the genus (fig. 4). Parasite in the gut-epithelium of *Tubifex* Müll. Stvanice, Czechoslovakia.

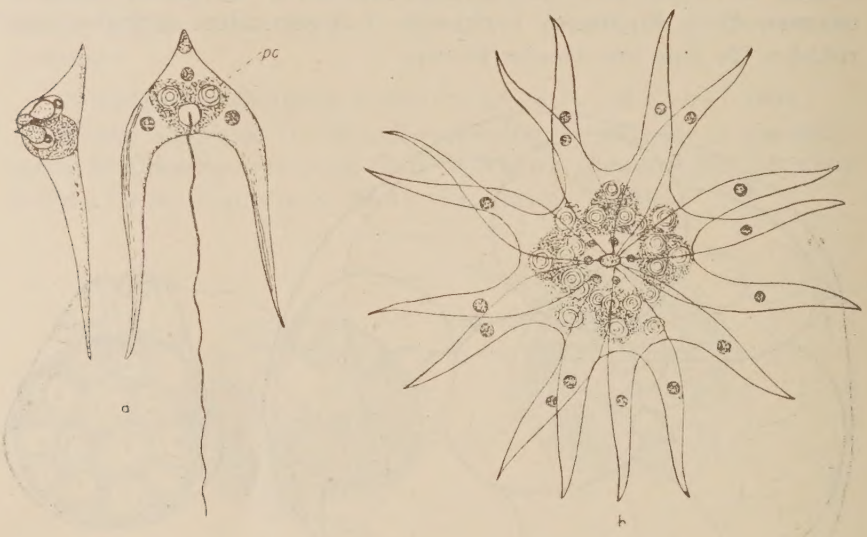

Fig. 4. *Synactinomyxon tubificis* Štolc: a — Spore from above, pc — polar capsule; Spores joined together. After Štolc.

V. Genus: *Guyénotia* Naville 1930.

Epispore with three equal, finger-like processes which are longer than the diameter of the spore. Sporoplasm multinucleate. The envelope of the pansporocyst with 4 nuclei. 1 species.

1. *Guyénotia sphaerulosa* Naville 1930.

Spores globular (fig. 5). Epispore with 3 finger-like processes of an equal length, longer than the diameter of the spore. The diameter of the spore is 15 μ, the length of the processes in the ripe spore 40 μ. Polar capsules are pear-shaped, measure 6×5 μ and open at the suture line, $2^1/_2$ μ from the apex of the anterior pole. Sporoplasm of 32 nuclei. Parasite in the gut-epithelium of *Tubifex tubifex* Müll. Found in Luc-sur-Mer (Calvados).

VI. Genus: *Raabeia* g. n. *

Epispore with three long, pointed and curved processes arising from the epispore without a style.

1. *Raabeia gorlicensis* g. n., sp. n.

Spore with three long processes of the epispore, each measuring 170 μ. The processes are evertible, but are invaginated while the spore is in the pansporocyst (fig. 6), their shape is curved and gradually narrowing towards the tips as in *Triactinomyxon ignotum*, they do not however form a style but arise directly from the middle, equatorial part of the sporoplasm. The sporoplasm is oval and measures approx. 35 μ.

Parasite in the body-cavity of *Tubifex tubifex* Müll. Found by the author in the river Odra and Ropa (Carpatians, Poland).

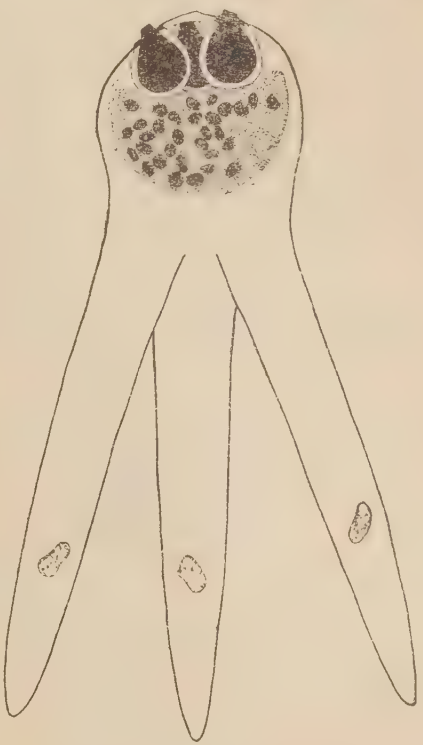

Fig. 5. *Guyénotia sphaerulosa* Naville. Spore, semidiagrammatically. After Naville.

VII. Genus: *Siedleckiella* Janiszewska 1953

Spores united into a hexahedrid reticulum. Epispore tripodal with obtuse arms or finger-like processes. 2 species.

1. *Siedleckiella silesica* Janiszewska 1952(53).

Epispore anchor-like with obtuse arms. The spores (fig. 7a) are joined together, the ends of each arm of the envelope of one spore

* I name this genus to the memory of the polish protozoologist, prof. dr. Henryk Raabe. A more detailed description of the structure and biology of these n. g. and n. sp. will appear separately.

Fig. 6. *Raabeia gorlicensis* g. n., sp. n. Ripe spore. Original.

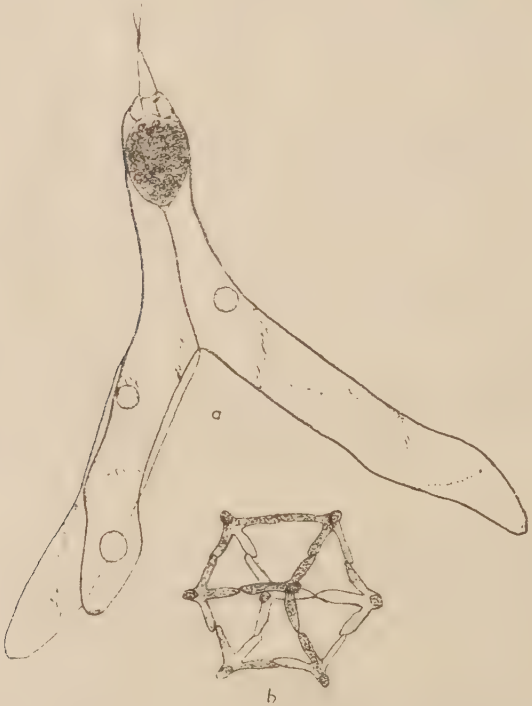

Fig. 7. *Siedleckiella silesica* Janiszewska: a — Ripe spore; b — United spores forming net. After Janiszewska, 1953.

joining the arm of a different spore and forming thus a cube-shaped reticulation (fig. 7b). Sporoplasm barrel-shaped, contains over 100 nuclei and measures 30—40 μ. The length of the entire spore is 185—205 μ. Lives in gut-epithelium of *Tubifex* sp. Inundation areas of the Odra river in the surroundings of Wrocław.

Fig. 8. *Siedleckiella antonii* Janiszewska 1954—55. Spore joined together with other spores. After Janiszewska, 1954.

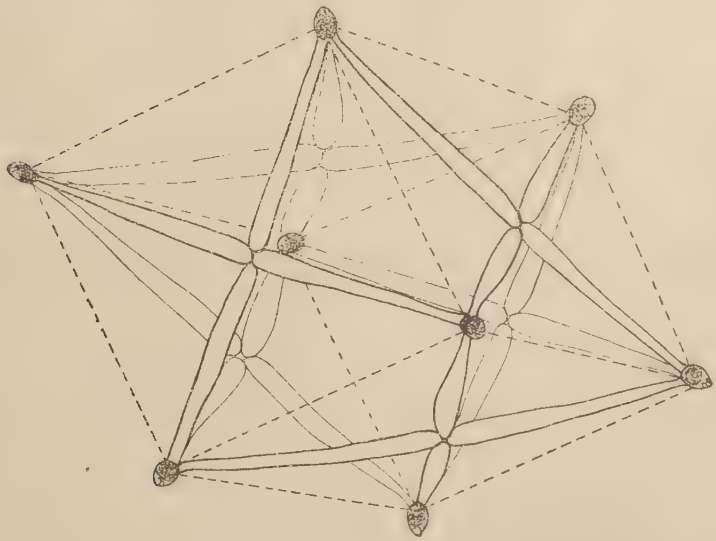

Fig. 9. *Siedleckiella antonii* Janiszewska 1954—55. A model of the net formed by the united spores. After Janiszewska, 1954.

2. *Siedleckiella antonii* Janiszewska 1955

The long finger-like processes of the epispore measure 130 μ. The spores form a three-dimensional reticulation, each process of one spore joining three processes of three different spores (fig. 8, 9). Sporoplasm barrel-shaped and multinuclear. Lives in the body-cavity of *Limnodrilus claparèdeanus* Ratz. Found in inundation areas of the Odra river near Wrocław.

VIII. Genus: *Triactinomyxon* Štolc 1899.

Epispore anchor-shaped with three long, pointed arms. Sporoplasm contains 8—100 nuclei or sporozoites and has an elongated, conelike shape. 5 species.

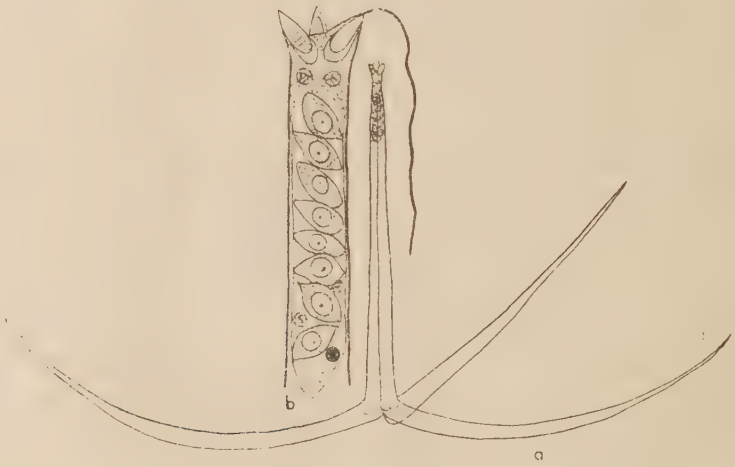

Fig. 10. *Triactinomyxon ignotum* Štolc: a — spore; b — upper part of the spore with sporozoites. a — after Štolc, b — after Léger.

1. *Triactinomyxon ignotum* Štolc 1899.

With the characters of the genus. The ripe spore contains 8 mononuclear sporozoites (fig. 10). The spore measures 110—165×11—15 μ. The sporoplasm is 20—30 μ long. Sporozoites 4,5×3,5 μ. Lives in the gut-epithelium of *Tubifex* sp., Štolc-Stvanice, Czechoslovakia. Granata: Fiume, Greve, Florence; *Tubifex tubifex* Müll., Léger: Grenoble, Mackinnon and Adam: Themse, London.

2. *Triactinomyxon magnum* Granata 1923.

With the characters of the genus. Epispore with exceedingly long arms, the whole measuring about 500 μ. Sporoplasm contains 16 nuclei. Lives in the gut-epithelium of *Limnodrilus udekemianus* Claparr. Fiume, Greve, Florence.

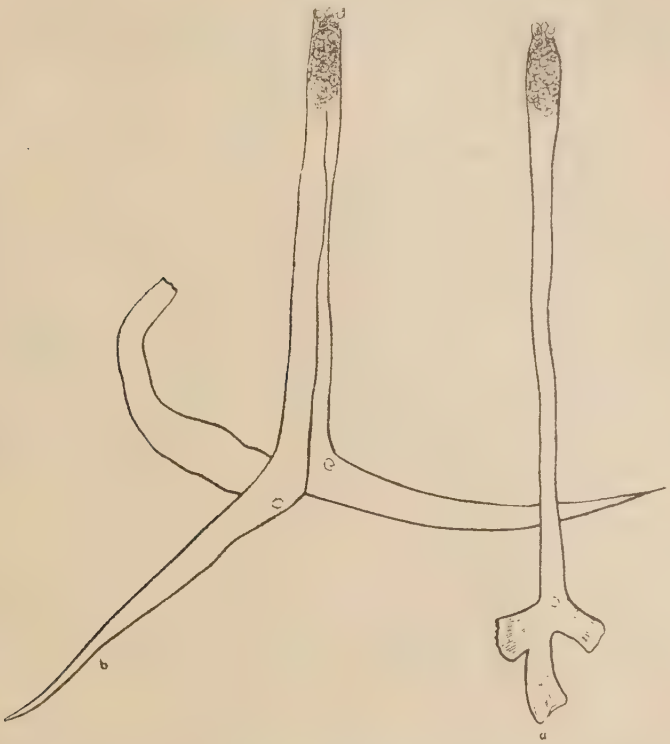

Fig. 11. *Triactinomyxon légeri* Mackinnon-Adam, a — with processes expanded; b — with two of the processes fully and the third partially expanded. After Mackinnon and Adam.

3. *Triactinomyxon légeri* Mackinnon et Adam 1904.

With the characters of the genus. Spores 90—140×11—16 μ. The sporoplasm 15—20 μ. The ripe spore contains 24 sporozoites ranged by 8 in three longitudinal rows (fig. 11—12). Sporozoites 2,7×2,2 μ. They contain a comparatively large nucleus (1.3 μ). Spores after emerging from the pansporocyst contain 12 binucleate bodies resulting from the fusion of two sporozoites. Lives in the gut-epithelium of *Tubifex tubifex* Müll. Found in London.

4. *Triactinomyxon dubium* Granata 1924.

Synonymous with *Triactinomyxon* sp. Léger 1904. With the characters of the genus. Sporoplasm splits into 32 sporozoites. Lives in the gut-epithelium of *Tubifex tubifex* Müll. Found in Grenoble.

5. *Triactinomyxon mrázeki* Mackinnon et Adam 1924.

The cone-shaped part of the envelope is longer than in *Tr. légeri* (fig. 13). Spore 150 × 12 μ; sporoplasm 25—65 μ, contains 50—100 mo-

Fig. 12. *Triactinomyxon légeri* Mackinnon-Adam: a — Living pansporocyst containing eight spores; b — Invaginated tips of processes of the sporal envelope. After Mackinnon and Adam.

nonuclear sporozoites. The nuclei of the sporozoites somewhat smaller than in *Tr. légeri*. Lives in the gut-epithelium of *Tubifex tubifex*, London.

6. *Triactinomyxon ohridensis* Georgević 1940.

Length of spore 120—140 μ. The endospore measures 20—30 × 7—8 μ. Outer envelope with 6 nuclei. Sporoplasm splits into 8 sporozoites. Living in the gut-epithelium of *Tubifex ohridensis* St. Naoum, near Lake Ochrida.

7. *Triactinomyxon petri* Georgević 1940?

From the description given by this author it appears that he dealt with two separate species but described them as a single one. His

figures 11 and 12 show two different species. The description of the envelope, on which to a great extent systematics are based, is incomplete and inadequate. Found in Lake Ochrida. Host: *Lumbriculus* sp.

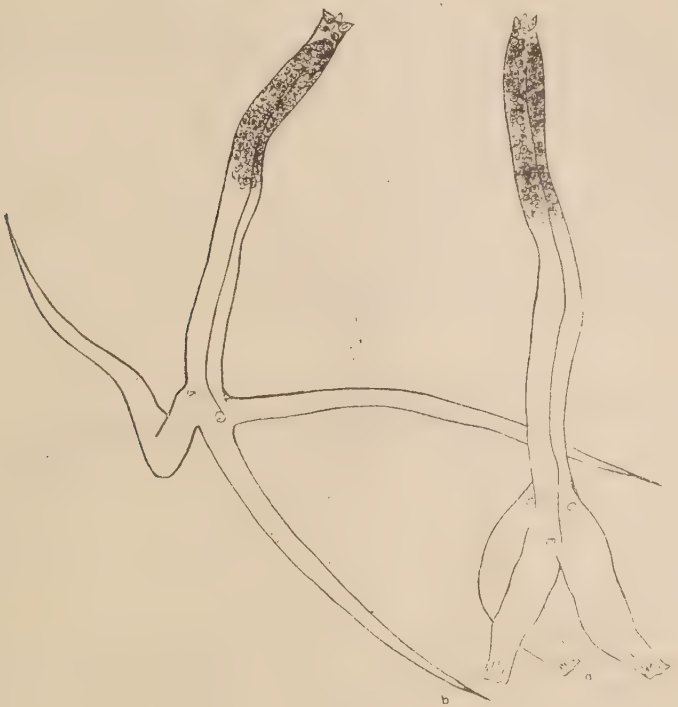

Fig. 13. *Triactinomyxon mrázeki* Mackinnon-Adam. Spores with the processes partially (a) and fully (b) expanded. After Mackinnon and Adam.

IX. Genus: *Hexactinomyxon* Štolc 1899.

Spore anchor-shaped with 3 double, in total 6 arms (fig. 22). Sporoplasm with many large nuclei. 2 species.

1. *Hexactinomyxon psammoryctis* Štolc 1899.

With characters of the genus (fig. 14). Lives in the gut-epithelium of *Psammoryctes barbatus* Grube. Stvanice island, near Prague.

2. *Hexactinomyxon hedvigi* sp. n. *)

Style of the epispore much shorter (fig. 15), bearing six processes thicker and shorter than in *Hexactinomyxon psammoryctis*. Style together with the sporoplasm measures 136—140 μ, the processes arising from the style are 152—180 μ long. The sporoplasm is barrel-shaped.

Lives in the gut epithelium of *Tubifex tubifex* Müll. Found by the author in the river Ropa (Carpatians, Poland).

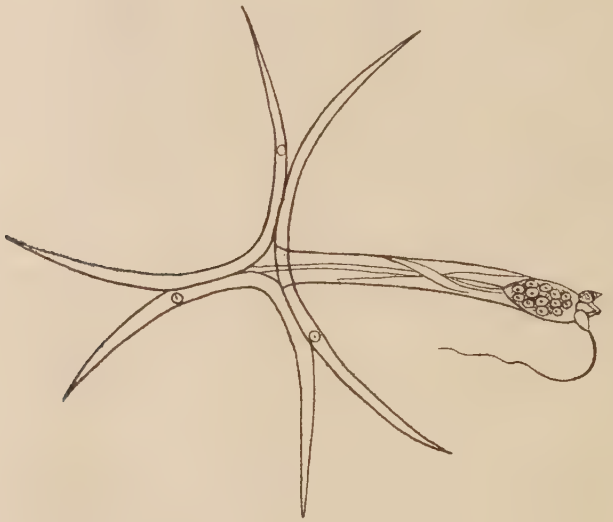

Fig. 14. *Hexactinomyxon psammoryctis* Štolc. Ripe spore. After Štolc.

Development

The development of the *Actinomyxidia* is as yet incompletely known. and there are some points awaiting further study. We can distinguish three phases in the development of the *Actinomyxidia*.

The first and least investigated phase comprises the beginning of infection and might be called the vegetative phase, i. e. a stage beginning with the liberation of the sporozoite from the spore and ending with the formation of the pansporocyst. As stated by Caul-

*) A more detailed description of the structure and biology of these new species will appear separately.

l e r y and M e s n i l (1904) the *Actinomyxidia* are deprived of a real vegetative life similar to that of the *Myxosporidia*.

The second phase, that of gametogenesis leading to the formation of the gametes and their copulation, is the sexual phase and is relatively well studied. In all studied forms this phase follows the same pattern.

The third phase comprises sporogenesis, i. e. the formation of spores and sporozoites and might be called a phase of multiplication.

Fig. 15. *Hexactinomyxon hedvigi* sp. n. Ripe spore. Original.

Almost all workers agree that the *Actinomyxidia* have no schizogony and that this process is supplanted in many forms by the formation of a great number of sporozoites (J í r o v e c 1940). The faculty of autoinfection admitted by certain authors might to a certain degree also make up for the lack of schizogony — autoinfection leading to a very intense infection and thus to the formation of great many sporozoites increasing the chance of infection.

G e o r g e v i ć (1940) thinks that in *Actinomyxidia* just as in *Myxosporidia* schizogony does take place but is simpler and less differentiated.

The mature spore contains a number of sporozoites. This number is stable and characteristic for the several species, varying only

within certain fixed limits. The sporozoites have one or two nuclei (two in *Tetractinomyxon*). The development of the sporozoite leads to the formation of a pansporocyst containing 8 spores.

Gametogenesis

The first developmental stages of the sporozoite are very hard to detect and are therefore still incompletely investigated. In *Tetractinomyxon*, according to Ikeda, the spore contains always a single binucleate sporozoites. Also in the tissues of the host he found always only such elements with two unequal, closely apposed nuclei. The binucleate elements unite by twos and form a four-celled group which gives rise to a pansporocyst. The two smaller cells form the envelope of the pansporocyst and the two larger ones, lying inside the envelope, constitute the mother-cells of the gametes.

The first workers on the development of the *Actinomyxidia* — Caullery and Mesnil — found in *Sphaeractinomyxon štolci* that the spore contains a large number of mononuclear elements. The earliest developmental stages upon which they came in their studies were binucleate forms, of unknown origin, as to which they put forward two hypotheses: The binucleate forms arise 1) by plasmogamy from mononucleate sporozoites, or 2) by division of the nucleus of the sporozoite. Other workers, for instance Léger, Granata, Mackinnon and Adam found at the beginning of infection also binucleate forms only. Mackinnon and Adam hold the opinion that binucleate forms arise by a more or less close union of two cells. Those uniting cells in some *Actinomyxidia*, e. g. *Tetractinomyxon*, stem from two different spores, in others, as e. g. *Triactinomyxon légeri* and most probably *Tr. ignotum*, they come from the same single spore. Each of the united cells take part in the formation as well of the envelope of the pansporocyst as of its contents i. e. formation of the gametes, so that half the gametes come from the one, and the other half from the second cell.

Granata is, like Caullery and Mesnil, of the opinion that two hypotheses account for the possible origin of binucleate elements.

I° the binucleate elements arising by division of the nucleus of a single sporozoite.

II° the binucleate elements arise by fusion of two sporozoites.

According to G e o r g e v i ć (1940) the binuclear stage is preceded by schizogony. The initial stage of schizogony would then be constituted by a mononuclear, globular element corresponding to a sporozoite. He found such elements in the lumen of the gut and particularly at the base of the gut epithelium in the investigated specimens.

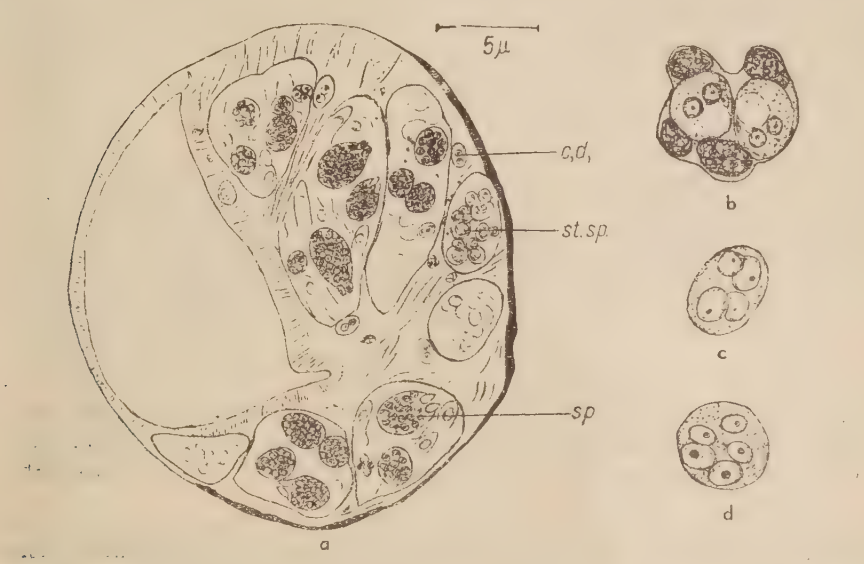

Fig. 16. *Siedleckiella silesica* J a n i s z e w s k a: a — Cross section through the gut of the infected *Tubifex* sp., c. d. — binucleate body, sp. — spore, st. sp. — developmental stages of spores; b — *S. antonii* J a n i s z e w s k a, two binucleate bodies together surrounded by lymphocytes of the host; c — *S. silesica* J a n i s z e w s k a, the second division of the binucleate body and the separation of the pansporocyst sheath; d — *S. silesica* J a n i s z e w s k a, next following stage, the three smaller nuclei belong to the sheath. After J a n i s z e w s k a 1954.

The elements go on dividing energetically by mitosis for a time and ultimately form mononuclear cells similar to schizonts. Binuclear bodies arise by division of the nucleus.

By division of a binucleate element arise 4 cells (fig. 16). Two of them separate as somatic cells of which the envelope of the pansporocyst is formed and the two remaining are propagative cells, of which arise gametes and later the spores (fig. 16d—17a). In some genera, as e. g. in *Guyénotia, Siedleckiella, Triactinomyxon magnum*

the two somatic cells divide once again forming a fourcelled envelope of the pansporocyst. The somatic cells grow, flatten out and close in upon the inner cells. This two- or four-celled envelope grows apace with the increasing number of the inner cells, its rôle is protective for the gametes, and later for the spores which develop within it, and it assimilates nutritive material supplied by the host.

The two inner cells are mother-cells of the gametes. Gametogenesis comprises three divisions of both inner cells. The cell called α by

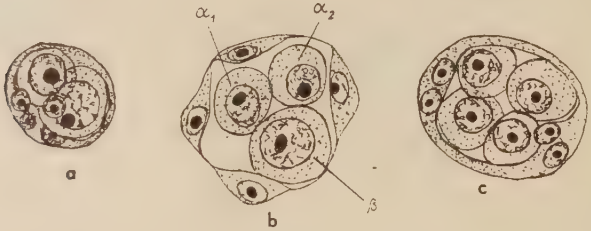

Fig. 17. *Siedleckiella silesica* Janiszewska: a — Pansporocyst, the four-celled sheath with two inner cells α and β inside; b — The first division of the α cell; c — The first division of the β cell. After Janiszewska, 1953.

the authors divides first, and division of the cell β lags behind. The cell β, which is late in dividing, is looked upon as the mother-cell of female gametes, the earlier dividing cell as the mother-cell of male gametes. Consequently, after the first division the young pansporocyst contains three inner cells α_1 α_2 and β (fig. 17a). The next division comprises the cell β and thus there are four inner cells (fig. 17c). The next two divisions, i. e. nr. 3 and nr. 4, comprise the α cells and there result 8 α cells and two β — we have thus α_{111}, α_{112}, α_{121}, α_{211}, α_{222}, α_{122}, α_{212}, β_1 and β_2 (fig. 18a). The two last divisions of the gametes lead to the formation of eight female gametes, and then we have in all the following gametes: α_{111}, α_{112}, α_{122}, α_{112}, α_{211} α_{221}, α_{212}, α_{222}, β_{111}, β_{121}, β_{122}, β_{112}, β_{211}, β_{221}, β_{212}, and β_{222}.

According to Granata gametogenesis comprises processes in which four phases can be discerned:

1) The phase of proliferation of the α cells, during which the cell β passes through its first division.

2) phase of growth of the cells.

3) phase of proliferation of the β cells, during which the α cells are ripening.

4) phase of ripening of the β gametes.

In the pansporocyst we have then eight male and eight female gametes (fig. 18b), of which each has a haploidal number of chromosomes. The process of chromosome reduction is still not definitely known and two differing views are being put forward. Léger (1904), Ikeda (1912), Granata (1924) and Mackinnon and Adam (1924) think that it comes to pass by expulsion of polar bo-

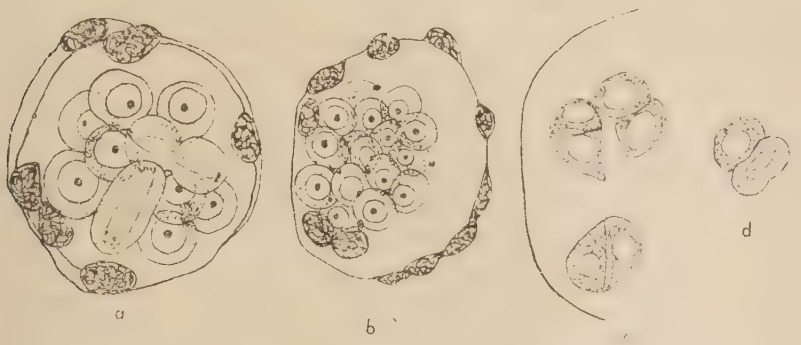

Fig. 18. *Siedleckiella antonii* Janiszewska: a — Pansporocyst with eight gametes α and the cells β_1 and β_2 dividing; b — Pansporocyst with eight gametes α and β; c — Zygote after the first division; d — Second division of the zygote. After Janiszewska, 1954.

dies. According to that view polar bodies are the small, globular bodies observed in the pansporocyst, lying on the outside of the cells, mostly in number of 16, in some forms e. g. *Triactinomyxon légeri* less than 16, whereas in *Triactinomyxon ignotum* they number 24—30. Granata (1924) thinks that their number, greater or lesser than 16, is the result of either the fusion of some bodies or their fission into two bodies. These bodies stain intensely with nuclear stains. in *Guyénotia sphaerulosa* according to Naville (1930). they appear in the pansporocyst very early, already at the stage of the two inner cells; in *Siedleckiella* according to my observation (1953), they appear only at the time of the two last divisions of the β cells, i. e. approximately at the stage of 14 cells.

Naville, who studied the chromosomal cycle in *Guyénotia sphaerulosa* very thoroughly, thinks that these bodies are nucleoli

expulsed from the cells during mitosis, because 1) the bodies stain similarly to the nucleoli, 2) during kinesis one sees nucleoli migrating to one of the poles, 3) bodies of a similar kind are seen in the pansporocyst while in the stage of two inner cells (α and β) and at a time when meiosis could not yet have taken place, 4) the number of the bodies is not stable. He calls them "chromatoid bodies". Up to date none of the investigators was able to observe them in statu nascendi.

I expressed (1953—54) the hypothesis that the appearance of the bodies is linked up with the flat or globular inclusions found in the gametes or their mother-cells and which stain deeply with nuclear stains. They lie mostly on the circumference of the cell. They were observed by Caullery and Mesnil (1905), Granata (1924), Jírovec (1940) and Janiszewska (1955). Granata thinks that they are built of chromatin and that they should be looked upon as chromidia. In *Siedleckiella* however I observed that in some of the cells the inclusions lay close to the surface, covered only by a thin film of protoplasm and that in some instances the film was partly split and the inclusion lay on top of the cells. The shape of the chromatoid bodies is, as I was able to observe, at first flat and elongated, similar to the shape of the inclusion and is beset with small floccules as if of freshly detached protoplasm. Further cytological studies are yet needed to elucidate the origin and rôle of the inclusions.

Naville (1930) in *Guyénotia sphaerulosa* and Jírovec (1940) in *Sphaeractinomyxon ilyodrili* have counted the chromosomes during the several divisions and came to the conclusion that the chromatin reduction in the cells α and β is of the same kind as in spermatozoa of the *Metazoa* i. e. the first division of α and β is gonial, diploidal and the second is a heterotypical meiosis i. e. leading from the diploidal stage with e. g. 4 chromosomes to a haploidal with 2 chromosomes. The third division is homeotypic and strictly haploidal, leading to the formation of ripe gametes.

The first formed gametes i. e. the α cells are in some species somewhat smaller than the female β gametes. In other species α and β are of equal size differing only in the α cells ripening earlier than the β, that is having a different rythm of division. Naville stresses the fact that the developmental cycle during maturation of the gametes is marked by precocious sexualization, apparent already during the gonial kineses, which leads to the segregation of two lines — the

male and the female. Indeed this advance in sexualization connected with the process of meiosis is a particular feature of the developmental cycle in the *Actinomyxidia.*

An opposite view on gametogenesis is upheld by Georgević (1940). According to him the stage with 16 inner cells is not a sexual stage. He maintains that these cells are diploidal, 8 of the cells being gametocytes and the remaining 8 cells representing the mother-cells of the spore envelope. Definitely sexual processes, i. e. the ripening of the gametes and a haploidal stage take place in the spore. He thinks that the real gametes are either the sporozoites or the nuclei found in the sporoplasm.

Sporogenesis

All investigators, with the exception of Léger, have seen copulation ensuing after the formation of 16 gametes. Léger (1904), although he described chromatin reduction during meiosis, did not notice the copulation of gametes and is of the opinion that eight cells issued from α^3 form the cells of the spore envelope and that the eight issued from β^3, the bulk of the sporozoites during the consequent divisions. It follows that he either does not accept or does not know the sexual aspect of these processes. According to Granata (1924), plasmogamy takes place during copulation. Kariogamy with ensuing formation of a synkarion was observed only in *Tetractinomyxon* and *Neoactinomyxon.* Most likely the nuclei of the gametes produce a kariokinetic spindle only when they come into close contact. Then eight zygotes, the sporoblasts, are formed which develop into spores. The spore is made up of the outer and the inner envelope and of a sporoplasm containing numerous nuclei, or of single sporozoites. My last investigations (1953—54) prove that the inner envelope is present not only in *Tetractinomyxon* Ikeda, but in all *Actinomyxidia* known at present. The outer envelope is composed of six cells, three cells forming the polar capsules and three cells the envelope proper, the inner envelope is composed of 1—3 cells. The sporoplasm in the majority of species is a syncytium formed by a varying number of cells. The formation of these parts of the spore is shown in a diagramatic presentation of divisions of the zygote in *Tetractinomyxon intermedium.* The fig. 21, 22 shows that the first division of the zygote leads to the formation of two differentiated cells, of which one in the following divisions forms only the cells of the envelope of the spore, while the second gives in its

next division again two different cells, inasmuch as one of them is purely somatic; this cell divides once again and forms the two cells of the polar capsules. The other cell in its next division gives issue to one cell of the inner envelope and to another which will produce sporozoites in a number characteristic for each of the species.

Granata (1924) recognizes in the development of sporoblasts two phases: 1) a phase of development and 2) a phase of proliferation. According to him the cells of the envelope and the propagative cells are formed during the phase of proliferation. In *Tetractinomyxon* this process is analogous to that found in other *Actinomyxidia*. In *Tetractinomyxon* there are 7 consecutive divisions resulting in the formation of seven cells of the envelopes (diagram I) i. e. 3 epispore cells, 1 endospore cell and 3 cells of the polar capsules, as well as a single propagative cell. In all instances the formation of the sheath-cells is in advance of the formation of the polar capsule cells.

In the phase of development Granata distinguishes a trophic phase, i. e. a period at which the bulk of the propagative cells lies still near the circumference of the pansporocyst envelope and has not yet penetrated into the envelope of the spore (see below).

The majority of investigations have noticed in the process of spore formation that two independent masses of cells appear after the first divisions of the zygote. One mass composed of six cells lies in the centre of the pansporocyst, and the second — of one or four nuclei — lies peripherally. The first gives rise to the envelope of the spore together with the polar capsules, and the second to the sporozoites. Next the sporoplasmatic mass penetrates the already formed envelope and pursues its further development inside it. In *Guyénotia* the penetration takes place when the protoplasmatic mass is composed of 8 nuclei, in *Sphaeractinomyxon* — when its number is greater. The position of the protoplasmatic masses near the surface of the pansporocyst assures, according to the authors a better nutrition.

It was stated on the other hand by Mackinnon and Adam that the envelope of the spore and the sporoplasm develop in close conjunction and do not separate. They think that the observations of other workers are erroneous and can be accounted for by the great difficulties encountered in studying microscopical sections of maturing pansporocysts and by the possibility of artefacts during fixation caused by shrinkage and bursting of the maturing spores.

Some investigators have observed in the sporoplasm, besides small nuclei belonging to the sporozoites. one or two larger nuclei, which they called somatic or residual nuclei (noyaux résiduels). N a v i l l e and J í r o v e c state that in mature spores there are no residual nuclei. Up to date however investigations have either failed to work out some of the stages or have interpreted them erroneously. My

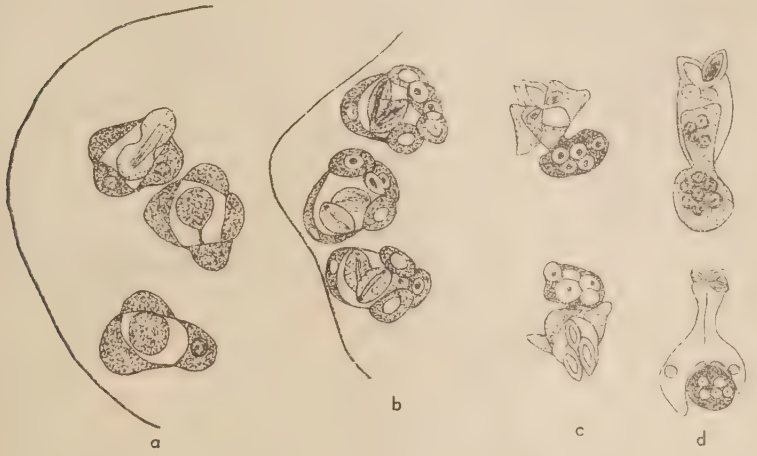

Fig. 19. *Siedleckiella silesica* J a n i s z e w s k a: a — Sporogenesis, the division of the fourth cell into the endospore cell and (inside) the sporoplasm cell; b — Sporogenesis, fission of the cells of the epispore and of the cells of the sporoplasm inside the endospore; c — Two young spores: Polar capsules in the epispore are formed, the processes are rudimentary. The sporoplasm surrounded by the endospore hangs down from the epispore on a constricted stalk; d — A young spore. After J a n i s z e w s k a. 1954—55.

latest studies of the development of *Siedleckiella* have proved that sporogenesis follows quite a different pattern. The three first divisions of the zygote give issue to four cells, of which three take up a position under a sharp angle to each other, forming thus a pyramid and later, after one division of each cell, give rise to the outer envelope (fig. 18c—19a). The fourth cell occupies a place at the base of the pyramid (fig. 19a) and encloses from below the space under the pyramid. The cell divides and gives up into that space the fifth cell which is the rudiment of the sporoplasm or sporozoites (fig. 19a). The fourth cell, enclosing the fifth, becomes flat and assumes the shape of a pouch in which lie the dividing cells of the sporoplasm

(fig. 18b). It forms thus an inner envelope of the sporoplasm. The nucleus of that inner envelope divides again once or twice, and the plasm increases its volume. Thus a syncytium is formed similar to that of the envelope of the pansporocyst. The nuclei of the inner envelope, the endospore, correspond to the somatic nuclei of the authors (noyaux résiduels, somatische Kerne). Simultaneously with these processes the cells of the pyramid divide and become differentiated into the three cells of the polar capsules and the three cells of the proper outer envelope. When the outer envelope reaches its perfect shape it is invaded by the sporoplasm developing and dividing together with the inner pouchlike envelope. The two masses of simultaneously developing cells are united during the whole time and this connection can be either broad (*Siedleckiella antonii*) or very narrow (*Siedleckiella silesica*) (fig. 19 c, d), depending upon the structure of the envelope and the volume of the sporoplasm. In *Sphaeractinomyxon* and *Neoactinomyxon* the sporoplasm ensheathed by the endospore lies on the circumference of the pansporocyst, while the forming epispore lies in its centre. In *Siedleckiella* the penetration of the epispore by the sporoplasm is a gradual process (fig. 20 a, b). The penetration is due either to a amoeboid movement of the sporoplasm or to a dehiscence of the envelope, or to the concurrence of both these factors. Štolc (1899) has observed in *Hexactinomyxon* the sporoplasm coming out of the sheath and moving about amoeboidally, while in *Triactinomyxon* it moved about inside the spore. Léger (1904) and Granata (1924) again have observed that the spore shows a dehiscence in the hinder part of the envelope. I have seen that in young spores of *Siedleckiella* the envelope becomes easily dehiscent, forming a kind of rupture, when under artificial conditions the pansporocyst bursts and the yet not quite mature spores get into water (fig. 20 c). When mature spores get into water a rupture is never formed.

When comparing the stages in the genus *Siedleckiella* described by me (1953 a) with drawings of corresponding stages in papers of the several authors I came to the conclusion that spore formation in all *Actinomyxidia* follows the same pattern i. e. that found by me in *Siedleckiella*. The assumed absence of the inner envelope, the endospore, in the *Euactinomyxidae* and the apparently separate development of the outer envelope of the sporoplasm in the beginning of spore formation are due to an erroneous interpretation of these stages. The connexion between the developing envelope and the

sporoplasmatic mass is hardly visible, when one studies the appropriate stages either on microscopical sections only or on smears of spores still contained in the pansporocyst, because then the cells are crowded in the tiny space inside the pansporocyst and they stick together under the influence of fixatives. The connexion is visible in spores taken out of the pansporocyst in vivo (fig. 19 d). An appro-

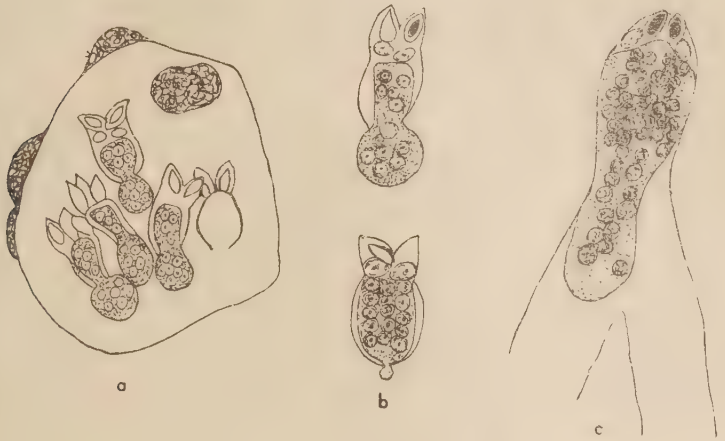

Fig. 20. *Siedleckiella antonii* Janiszewska: a — Spores with the sporoplasm gradually entering the epispore, the processes of the epispore omitted; b — Spores as on the fig a; c — Spore with the sporoplasm inside. After Janiszewska, 1954—55.

priate material for investigation is needed to enable a thourough study of all the divisions and the consecutive stages, but such material is rather hard to obtain, as one generally finds one stage predominant at a given time.

The extraordinary development of the sporoplasm in *Actinomyxidia*, which in initial stages is as if evaginated out of the envelope is may be due to a difference in the mechanism of development of the two parts of the spore. The cells of the epispore having stopped to divide, begin to grow in size energetically and to specialize, while the cells of the sporoplasm remain in an embrional state and divide many times (in dependence of the number of sporozoites, characteristic of each species); they differentiate only after having penetrated the completely formed envelope. This may have also

a trophic aspect as G r a n a t a has rightly remarked, for these two simultaneously, divergently and energetically developing cell complexes might compete for nourishment and a better access to the source of nourishment might alleviate that competition. Between the development of *Tetractinomyxon* and of the other genera there is,

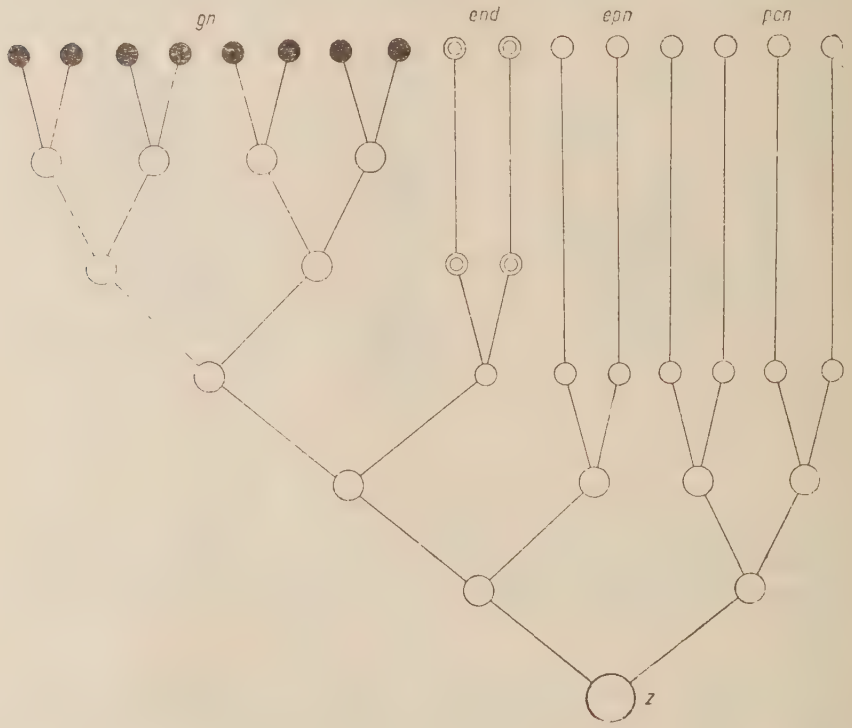

Fig. 21. Diagram of the developmental cycle in *Tetractinomyxon intermedium* I k e d a: I—X — development of the pansporoblasts, VIII—X — maturation of the gametes and their copulation, XI—XVI — formation of the spore. gc. — nuclei of the amoeboid sporozoite which arise from g (XV); pcn. — nuclei of the polar capsules; end. — nucleus of the endospore; epn. — nucleus of the epispore. After I k e d a.

a mentioned above, no basic difference but only a difference in the number of sporozoites. *Tetractinomyxon* having the smallest number (fig. 21 a. 22).

The uniformity of the development stages in the *Actinomyxidia* is an argument in favour of their monophyletic origin. The struc-

ture is simplest in the genus *Tetractinomyxon* I k e d a, the differentiation in the other forms followed two lines — one of a multiplication of sporozoites and the other of a specialization in the structure of the envelope.

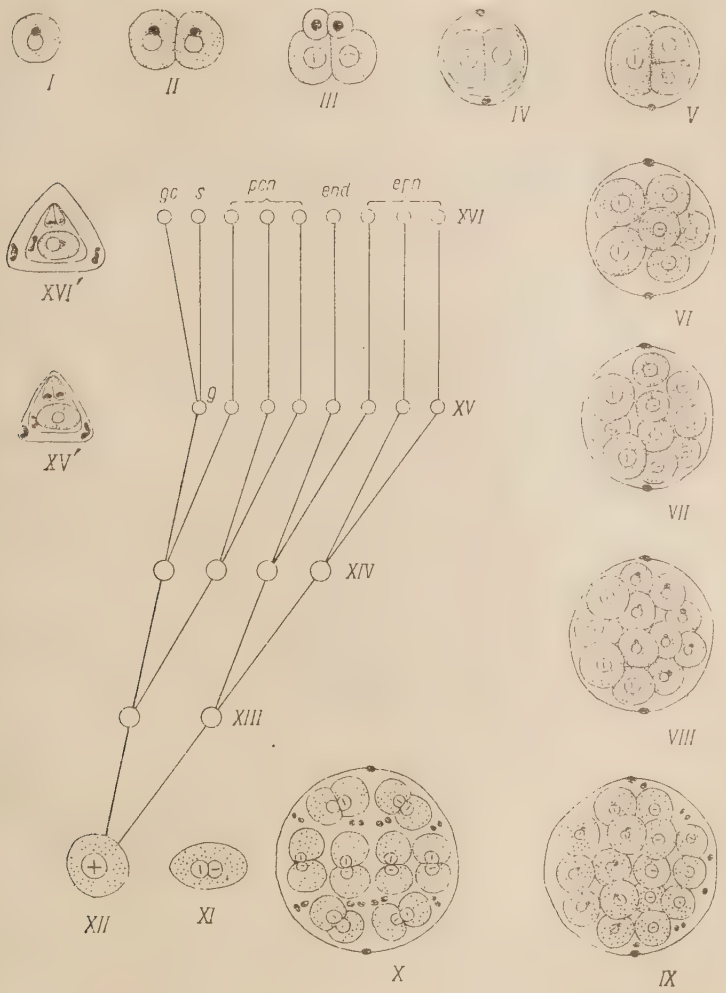

Fig. 22. Diagram of the sporogenesis in *Triactinomyxon ignotum* Š t o l c: z. — nucleus of the zygote; epn. — nuclei of the epispore; pcn. — nuclei of the polar capsules; end. — nucleus of the endospore; gen. — nuclei of the sporozoite. Original.

The *Actinomyxidia* show much resemblance in the process of fertilization and spore formation to the *Myxosporidia*. The structure and the development of the spore is however much more intricate. It is unknown whether the *Actinomyxidia* have vegetative reproduction in the form of schizogony; most authors think it not likely.

Methods of study

Mature spores are best studied in vivo, stained vitally with methylens blue or neutral red. All details of structure of the delicate and transparent envelope become then visible, which in current microscopical preperations are obscured by shrinkage. Sporogenesis is best studied on smears, after fixing with corrosive sublimate and staining with haematoxylin (Delafields, Heidenhains etc.), for me generally get then the pansporocyst with its entire content of all appropriate stages of division. For study of the chromosomal cycle and gametogenesis microscopical sections carried out by current methods and stained with haematoxylin and eosin are very useful.

The material for investigation, i. e. infected *Oligochaeta*, are collected from the bottom of ponds, lakes, inundation areas of rivers and other water basins by a small-meshed hand-net of a current type. The collected mud is washed on a sieve, with meshes of maximally 0,6 mm. Under a microscope or a magnifying glass we look for the *Oligochaeta* in the washed sediment. Specimens infected by parasites of the gut are noticeable by the gut being distended at the place of infection to a more or less marked degree, depending on the state of infection and the developmental stage of the parasite. The body-cavity parasites are readily discerned, for they swimm about slowly in the coelomatic fluid.

Author's address:
Muzeum Przyrodnicze Instytutu Zoologicznego
Wrocław, ul. Sienkiewicza 21.

LITERATURE

1. Caullery M. et Mesnil F. — Recherches sur les Actinomyxidies. I. *Sphaeractinomyxon štolci* C. et M. Archiv f. Protistenkunde, 6, 1905.
2. Georgević I. — Sur *Sphaeractinomyxon danicae* n. sp., Actinomyxidie parasite d'un Oligochète du lac d'Ochrida. C. R. séans. Acad. Sci. Belgrade, 207, 1940.
3. Georgević I. — Recherches sur les Actinomyxidies. 2. *Triactinomyxon ohridensis* n. sp. Bull. Acad. Sci. Belgrade, 6 B, 1940.
4. Georgević I. — Recherches sur les Actinomyxidies. 3. *Triactinomyxon petri* n. sp. Bull. Acad. Sci. Belgrade, 6 B, 1940.
5. Granata L. — Gli Attinomissidi. Morphologia — Sviluppo — Sistematica. Archiv f. Protistenkunde, 50, 1924.
6. Ikeda I. — Studies on some Sporozoan parasites of Sipunculoids. I. The life history of a new Actinomyxidian. *Tetractinomyxon intermedium* g. and sp. nov. Archiv f. Protistenkunde, 25, 1912.
7. Janiszewska J. — *Siedleckiella silesica* n. g. n. sp. *Actinomyxidia* (*Cnidosposidia*). Zoologica Poloniae, 6, 1, 1953.
8. Janiszewska J. — *Siedleckiella antonii* sp. n. Remarks on the sporogenesis in the genus *Siedleckiella* and in other *Actinomyxidia*. Zoologica Poloniae, 6, 2, 1954—55.
9. Jírovec O. — Zur Kenntniss einiger in Oligochäten parasitierenden Protisten. II. Über *Sphaeractinomyxon ilyodrili* n. sp. und *Neoactinomyxon globosum* Granata 1022. Archiv f. Protistenkunde, 94. 1940.
10. Léger L. — Considération sur le genre *Triactinomyxon* et les Actinomyxidies. C. R. Soc. Biol. Paris, 56, 1904.
11. Mackinnon D. L. and Adam D. I. — Notes on *Sporozoa* parasitic in *Tubifex*. I. The life-history of *Triactinomyxon* Štolc. Quart. Journ. of Microsc. Science, N. S., 68, 1924.
12. Mrázek A. — Referat Nr. 720: Štolc A., *Actinomyxidia*, nova skupina mesozou pributna *Myxosporidium*. Zool. Centralbl., 7, 17/18, 1900.
13. Naville A. — Le cycle chromosomique d'une nouvelle Actinomyxidie: *Guyénotia sphaerulosa* n. gen. n. sp. Quart. Journ. of Microsc. Science, N. S., 73, 1930.
14. Štolc A. — Actinomyxidies, nouveau groupe de Mesozoaires parent des Myxosporidies. Bull. Intern. Acad. Sci. de Bohème, 22, 1899.

STRESZCZENIE

Actinomyxidia (*Cnidosporidia, Sporozoa*) należą do pierwotniaków pasożytnych mało zbadanych. Autorka na podstawie własnych badań i przestudiowania literatury daje krótki rys dotychczasowych wiadomości o *Actinomyxidia*. Praca składa się z rozdziałów obejmujących: morfologię spory, ekologię, historię badań, systematykę, cykl rozwojowy, metody badań.

W opisie morfologii spory stwierdza autorka obecność dwóch osłonek (zewnętrznej i wewnętrznej epi- i endosporu) nie tylko u *Tetractinomyxon* I k e d a, lecz także u wszystkich innych rodzajów, na podstawie własnych badań. Osłonki zewnętrzne spory mają budowę przystosowaną do życia w planktonie. To przystosowanie służy do rozprzestrzeniania się tych form pasożytnych i jest przystosowaniem się do ekologii i etologii żywicieli. Autorka omawia lokalizację w żywicielu, działanie patologiczne, odporność spor na zmiany warunków środowiska, przypuszczalność samozarażenia, częstość występowania, specyficzność pasożytną itp.

Historia badań zawiera opis rozwoju systematyki i badań nad cyklami rozwojowymi. Na podstawie własnych badań nad sporogenezą stwierdza autorka, że wszystkie *Actinomyxidia* mają jednakowy cykl rozwojowy i wobec tego dotychczasowy podział na *Haploactinomyxidae* i *Euactinomyxidae*, oparty na obecności wewnętrznej osłonki u *Haploactinomyxidae* a rzekomym jej braku u *Euactinomyxidae*, jest nieodpowiedni. Obecnie znamy 9 rodzajów z 19 gatunkami, w tym 2 nowe rodzaje (*Siedleckiella* J a n i s z., *Raabeia* g. n.) i 4 nowe gatunki (*Siedleckiella silesica* J a n i s z., *S. antonii* J a n i s z., *Raabeia gorlicensis* g. n., sp. n. i *Hexactinomyxon hedvigi* sp. n.) odkryte przez autorkę. Lista żywicieli uwidoczniona jest na osobnej tabeli. Wszystkie dotychczas znane formy pochodzą z Europy. Bliżej nieoznaczone formy były znalezione przez K o f o i d'a w planktonie w Ameryce. Ponieważ żywicielami są *Tubificidae* i *Lumbricidae*, które są szeroko rozpowszechnione na kuli ziemskiej, dlatego należy się spodziewać, że pasożyty te mogą się znajdować także i w innych częściach świata.

Uproszczona przez autorkę tymczasowa systematyka przedstawia się następująco: Podgromada *Cnidosporidia*, rząd *Actinomyxidia*, do

którego należy 9 rodzajów; *Tetractinomyxon* Ikeda, *Sphaeractinomyxon* Caullery-Mesnil, *Neoactinomyxon* Granata, *Synactinomyxon* Štolc, *Guyénotia* Naville, *Siedleckiella* Janiszewska, *Raabeia* g. n., *Triactinomyxon* Štolc, *Hexactinomyxon* Štolc.

Cechy rodzajów zebrane są w formie klucza. Krótkie diagnozy gatunków składają się głównie z opisu budowy i wymiarów spor wraz z podaniem żywiciela i miejsca występowania.

Rozwój *Actinomyxidia* nie jest jeszcze kompletnie zbadany; są pewne luki, które czekają na opracowanie. W rozwoju można wyróżnić trzy okresy. Pierwszy, obejmujący początek zarażenia, tj. stadium od uwolnionego ze spory sporozoitu do wytworzenia pansporocysty, można nazwać okresem wegetatywnym i ten jest najmniej znany. Właściwe życie wegetatywne, takie jak u *Myxosporidia*, nie istnieje u *Actinomyxidia*. Drugi okres to gametogeneza, podczas której wytwarzają się gamety. Jest okresem płciowym zakończonym kopulacją gamet, stosunkowo dobrze zbadanym. Przebiega on u wszystkich form według jednego typu. Niejasną jest redukcja chromatyny u dojrzewających gamet. Część badaczy sądzi, że redukcja chromatyny przebiega w sposób podobny jak u gamet żeńskich w typie *Metazoa* tj. przez wydalenie ciałek kierunkowych, część sądzi, że podobnie jak u gamet męskich przez podział heterotypowy, przechodzący ze stadium diploidalnego w stadium haploidalne. Trzeci okres obejmuje sporogenezę, tj. wykształcanie się spor i sporozoitów; można by go nazwać okresem mnożenia się. Prawie wszyscy badacze, prócz Georgevića (1940), sądzą, że u *Actinomyxidia* nie ma schizogonii i że schizogonię zastępuje wytwarzanie się w sporach u wielu form dużej ilości sporozoitów. Brak schizogonii, zastępowałaby do pewnego stopnia zdolność do autoinwazji.

W dotychczasowych badaniach nad sporogenezą brak było pewnych stadiów, lub były one mylnie interpretowane. Mianowicie wielu badaczy sądziło, że sporoplazma, względnie sporozoity, rozwijają się początkowo osobno, niezależnie od osłonki zewnętrznej i że osłonkę wewnętrzną ma tylko rodzaj *Tetractinomyxon*. Badania autorki wykazały, że osłonka wewnętrzna powstaje już przy 4 i 5 podziale zygoty i że sporoplazma rozwija się początkowo w osłonce wewnętrznej poza osłonką zewnętrzną tak, jak to zauważyli inni badacze, ale nie osobno, niezależnie, lecz obie osłonki łączą się ze sobą za pomocą małego słabo widocznego połączenia.

Skoro osłonka zewnętrzna zostanie już całkowicie wykształcona, wówczas wnika do jej wnętrza sporoplazma wraz z otaczającą ją osłonką wewnętrzną.

Autorka sądzi, że ten zadziwiający rozwój sporoplazmy w początkowych stadiach jakby wynicowanej poza episporę, jest być może spowodowany różnicami mechanizmu rozwojowego tych obu różnych części spory. Być może, jak to zauważył G r a n a t a (1924), ma to także znaczenie troficzne i zabezpiecza lepszy dostęp pokarmu dla tych dwóch równocześnie silnie i odmiennie rozwijających się kompleksów komórek.

Między rozwojem *Tetractinomyxon* I k e d a a pozostałymi rodzajami nie ma zasadniczych różnic w budowie i rozwoju, są tylko różnice w ilości sporozoitów. *Tetractinomyxon* ma najmniejszą ilość sporozoitów.

Jednolitość stadiów rozwojowych u *Actinomyxidia* świadczy zatem, że są one pochodzenia monofiletycznego. Zróżnicowanie form szło w dwóch kierunkach: w kierunku zwiększania liczby sporozoitów i wyspecjalizowania się osłonki.

РЕЗЮМЕ

Actinomyxidia (*Cnidosporidia*, *Sporozoa*) принадлежат к еще мало исследованным паразитическим простейшим. Автор, основываясь на собственных и литературных данных, даёт короткий обзор сведений о *Actinomyxidia*. Работа состоит из следующих разделов, охватывающих: морфологию споры, экологию, историю наблюдений, систематику, жизненный цикл, метод исследования.

На основании собственных наблюдений, автор отмечает в морфологии споры присутствие двух оболочек (наружной и внутренней) эписпоры и эндоспоры не только у *Tetractinomyxon* Ikeda, но и у всех других родов. Наружные оболочки споры по своему построению приспособлены к жизни в планктоне. Эта приспособительность служит распространению этих паразитических форм и является их приспособленностью к экологии и этологии хозяев. Автор обсуждает их локализацию в теле хозяина, патологическую деятельность, устойчивость спор на изменение условий среды, предполагаемость самозаражения, учащенность появления, паразитическую специфичность и т. д.

В истории наблюдении заключается описание развития систематики и наблюдении над жизненными циклами. Основываясь на собственных исследованиях спорогенеза, автор констатирует одинаковый жизненный цикл у всех *Actinomyxidia* и считает, что существовавший до сих пор раздел на *Haploactinomyxidae* и *Euactinomyxidae*, основанный на наличии внутренней оболочки у *Haploactinomyxidae*, а кажущимся отсутствии её у *Euactinomyxidae*, не отвечает истине. Ныне известны нам 9 родов с 19 видами в этом числе 2 новые роды (*Siedleckiella* Janisz., *Raabeia* g. n.) и 4 новых вида (*Siedleckiella silesica* Janisz., *S. antonii* Janisz., *Raabeia gorlicensis* g. n, sp. n. *Hexactinomyxon hedvigi* sp. n.), описанные автором. Список хозяев отмечен на отдельной таблице. Все известные до сих пор формы выступают в Европе. Kofoid (Doflein 1916) нашел споры в планктоне в Америке. Так как хозяевами являются *Tubificidae* и *Lumbricidae*, которые широко распространены на целом земном шаре, можно ожидать, что эти паразиты найдутся и в других частях мира.

Упрощенная автором временная систематика представляется в следующим: подкласс *Cnidosporidia*, отряд *Actinomyxidia*, к которому принадлежит 9 родов: *Tetractinomyxon* Ikeda, *Sphaeractinomyxon* Caullery-Mesnil, *Neoactinomyxon* Grabata, *Synactinomyxon* Štolc, *Guyénotia* Naville, *Siedleckiella* Janiszewska, *Raabeia* g. n., *Triactinomyxon* Štolc, *Hexactinomyxon* Štolc.

Признаки родов собраны в виде ключа. Краткие диагнозы видов состоят главным образом из описи построения и размеров спор, совместно с подачей хозяина и мест нахождения.

Развитие *Actinomyxidia* еще полностью не исследовано: имеются некоторые проблемы, нуждающиеся в дальнейшей разработке. В жизненном цикле различаем три этапа. Первый, заключающий в себе начало заражения, т. е. стадию освобождённого из споры спорозоита до произведения панспороцисты, можно назвать этапом вегетативным. Этот этап менее всего исследован. Собственно вегетативная жизнь, такая как у *Myxosporidia*, у *Actinomyxidia* не существует. Второй этап, это гаметогенез, во время которого изготовляются гаметы. Этот половой этап, законченный совокуплением гамет, исследован относительно полно. Ход его развития у всех форм одного типа. Не совсем понятна редукция хроматина в созревающих гаметах. Некоторые исследователи полагают, что редукция хроматина протекает таким образом как в женских гаметах *Metazoa*, т. е. удалением направительных телец. Другие считают, что протекает она так как в мужских гаметах, путём гетеротипического деления переходящего из стадии диплоидальной в гаплоидальную. Третий этап охватывает спорогенез, т. е. формирование спор и спорозоитов; этот этап можно бы было назвать этапом размножения. Почти все исследователи полагают, что у *Actinomyxidia* не имеется схизогонии, а заменяет её выступание в спорах многих форм большого количества спорозоитов. Отсутствие схизогонии заменяла бы, в некоторых случаях, способность к автоинвазии.

До сих пор во всех наблюдениях над спорогенезом недоставало некоторых этапов, или же они были ошибочно истолкованы. А именно, многие исследователи полагали, что развитие спороплазмы или спорозоитов происходит в начале отдельно, независимо от наружной оболочки, а внутренняя оболочка находится исключительно у рода *Tetractinomyxon*. Наблюдения автора доказали, что внутренняя оболочка возникает уже при 4—5 дроблении

зиготы и что спороплазма с начала развивается во внутренней оболочке, вне наружной оболочки, так, как это заметили другие исследователи, но не отдельно, а обе оболочки связаны между собой посредством чуть заметного соединения. Как только сформируется окончательно наружная оболочка, во внутрь её внедряется спороплазма с окружающей её внутренней оболочкой.

Автор считает, что это удивительное развитие спороплазмы в начальных стадиях, как будто вывороченной на изнанку вне эписпор, происходит, быть может, по причине различия механизма развития этих обоих разных частей споры. Может быть, как это заметил Граната (1924), это имеет трофическое значение и обеспечивает лучшее проникновение питательных веществ в область этих двух комплексов клеток, развивающихся одновременно мощно и различно.

Между развитием *Tetractinomyxon* I k e d a а остальными родами не имеется существенных разниц в постройке и развитии; разница состоит только в количестве спорозоитов. *Tetractinomyxon* имеет найменьшее число спорозоитов.

Единородность стадий развития у *Actinomyxidia* свидетельствует об их монофилетическом происхождении. Разницование форм происходило в двух направлениях: в направлении увеличения количества спорозоитов и в выспециализировании оболочки.